The non-carnivorous leaf of *Darlingtonia californica*

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Keywords: Physiology: *Darlingtonia californica* leaf structure.

It is well known that *Darlingtonia californica* has two types of carnivorous leaves (Goebel 1891; Lloyd 1942). The juvenile carnivorous leaves consist of a long tube with a narrow, tongue-like extension that quite often curves down toward if not to the ground (Front Cover). The adult carnivorous leaves are a hooded tube with a fish tail or mustache-like extension. Large juvenile leaves can also be found on stolons or underground runners from adult plants. Horizontal small adult leaves can be found on juvenile plants. Developmentally, the juvenile leaves are not just simplified adult leaves (Franck 1976). Each type of leaf is adapted to a different set of prey.

What is not well known is *Darlingtonia* makes a flat, linear-lanceolate leaf as the first true leaf after the cotyledons in seedlings. I believe this linear-lanceolate leaf is not carnivorous because there are no obvious glands. Lloyd (1942) and Franck (1976) saw this leaf in their plants but interpreted it as a third cotyledon. It is not a cotyledon (Fig. 1). The leaf emerges after the cotyledons and its base wraps the apex inside the ring of cotyledons. Goebel (1891) recognized this leaf for what it is and noted it is the only case he knew of where such a leaf is produced within the Sarraceniaceae. It is also the only case I know of. The first true leaf produced by *Sarracenia* seedlings and all *Heliamphora* I am aware of, is a pitcher. The phyllodia of *Sarracenia* are not analogous to this *Darlingtonia* leaf. *Sarracenia* phyllodia are pitcher-derived, unifacial leaves (both sides are technically the outer facing, abaxial side of the leaf). Phyllodia are not normally produced in juvenile *Sarracenia*.

At first glance it would appear bizarre that *Darlingtonia* would maintain the developmental program to produce this third type of leaf. However, if this is the ancestral leaf then it could be present because the developmental program to produce a pitcher initiates after the leaf forms. To test this, 541 seedlings were observed, checking for plants that deviated from the first true leaf being linear-lanceolate and the second true leaf a pitcher. The results are shown in Table 1 and images of aberrant plants are in Fig. 2, Back Cover, and Brittnacher (2014). Among the Del Norte County, California, seedlings, 1% had three cotyledons and 1% had a leaf configuration different from typical. The Siskiyou County, California, seedlings had 4% with three cotyledons and 5% with atypical leaf configurations. About 1% of seedlings started pitcher development earlier than typical either producing a pitcher as the first true leaf or producing a leaf intermediate between a linear-lanceolate leaf and

Table 1. Presence of leaf types in seedling *Darlingtonia californica*. The Del Norte Co. seeds were from 3 locations. The Siskiyou Co. seeds were from one location. All the locations were on mountains although the Del Norte Co. locations were about 600 m elevation while the Siskiyou Co. location was 2000 m elevation. The numbers are too small to determine statistical significance between the locations.

	Cotyledons		First true leaf			Second true leaf		
County	Two	Three	Linear	Interm.	Pitcher	Linear	Interm.	Pitcher
Del Norte	439	4	439	1	3	1	0	442
Siskiyou	94	4†	96	2†*	0	0	4*	94

† One plant had both 3-cotyledons and an intermediate first leaf

* One plant had both intermediate first and second leaves

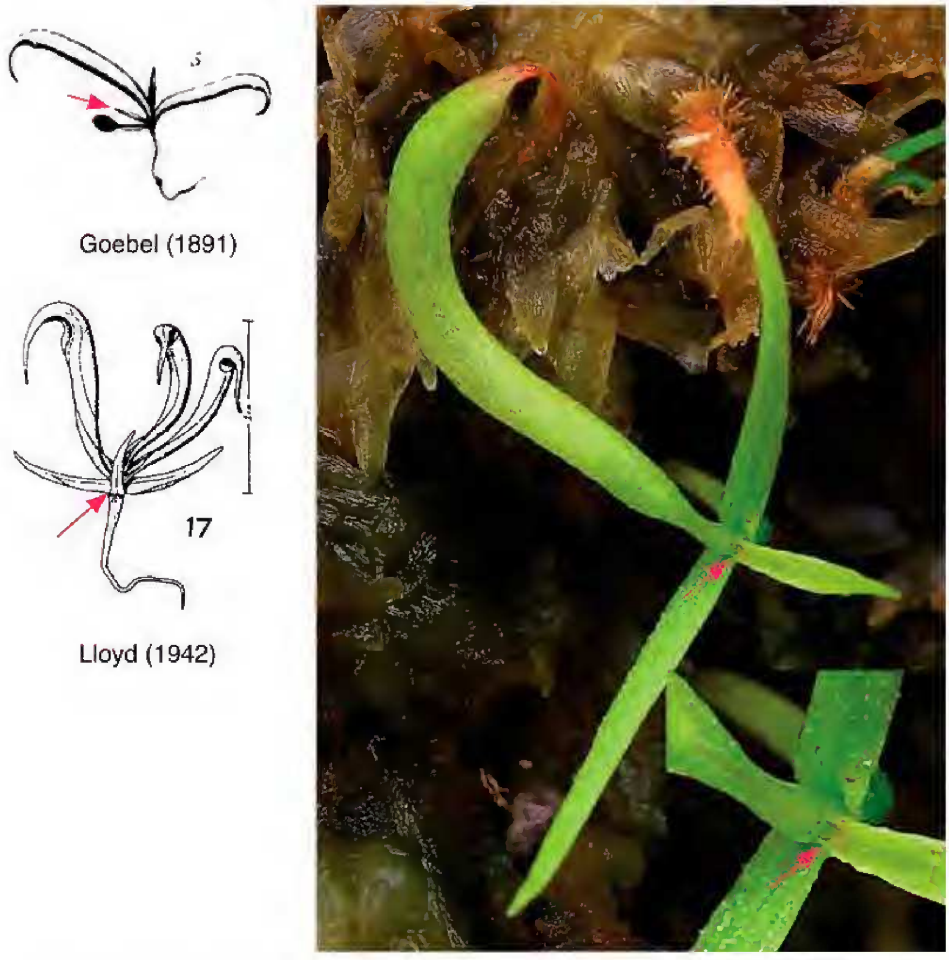

Figure 1: *Darlingtonia* seedlings. The drawing from Goebel (1891) shows the linear-lanceolate leaf shorter than the two cotyledons, one of which still has a seed attached. The Lloyd (1942) drawing shows the first true leaf as if it was a third cotyledon. The leaf should have been drawn enclosed by the cotyledons as shown by the image on the right. The inset details how the linear-lanceolate first true leaf wraps the apex within the cotyledons. Red arrows in photo indicate apex.

a pitcher. Another 1% started late, producing two linear-lanceolate leaves or an intermediate-type leaf as the second leaf. The exact numbers observed in this study are not necessarily indicative of the species as a whole since the seeds were collected from only a few individuals at each location.

As part of this study, I confirmed Harry Tryon's (personal communication) observation that the Mt. Eddy area, Siskiyou County seeds were larger with denser trichomes than seeds from coastal California, Oregon, and the Sierra Nevada of California (see Brittnacher 2014). It is not known if the differences in the seeds are the result of a unique difference in that population and whether a larger study would see differences in the seedlings.

The results of this study show the first true leaf in typical *Darlingtonia* seedlings appears to be an unmodified ancestral leaf. It is similar to the leaves of its relative *Roridula gorgonias* without the glandular hairs (see photos linked at http://cpphotofinder.com). The first true leaf not being a carnivorous leaf or derived from a carnivorous leaf in *Darlingtonia* appears to be unique among pitcher plants. *Sarracenia* and *Heliamphora*, sister genera to *Darlingtonia*, produce a juvenile pitcher as the first true leaf. Among non-relatives, the first true leaf in *Cephalotus* is a unifacial pitcher-derived

Figure 2: *Darlingtonia* seedlings with non-typical leaves: (a) three cotyledons instead of two, (b) second true leaf not a pitcher, (c) first true leaf a pitcher, (d) first true leaf intermediate between a linear-lanceolate leaf and a pitcher.

phyllode (see Brittnacher 2013) although a detailed study may show it can be either a pitcher or phyllode. Depending on the species or hybrid, the first true leaf of *Nepenthes* can range from recognizable adult-like pitchers to flattened leaf-like pitchers (see Brittnacher 2014).

Acknowledgement: I thank Mike Wang for seeds from two of the Del Norte Co. populations.

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